

New wheel microfossils of Ophiocistioidea and Holothuroidea (Echinodermata) from Japan

AKITO OGAWA^{1, 2, 4}, YUI TAKAHASHI³ & TOSHIHIKO FUJITA^{1, 2}

¹Graduate School of Science, The University of Tokyo, 7-3-1 Bunkyo-ku, Tokyo 113-0033, Japan

²Department of Zoology, National Museum of Nature and Science, 4-1-1 Amakubo, Tsukuba, Ibaraki 305-0005, Japan

³Earth Evolution Sciences, University of Tsukuba, 1-1-1 Tennodai, Tsukuba-shi, Ibaraki, 305-8572, Japan

⁴Corresponding author, E-mail: a-ogawa@kahaku.go.jp

Abstract

Microfossils in the form of wheels are characteristic of Holothuroidea and Ophiocistioidea (Echinodermata). Only a few wheel fossils have been ever reported without detailed description from Japan. Five wheel fossils were collected from the Carboniferous part of the Omi Limestone distributed in Itoigawa City, Niigata Prefecture, central Japan. The Limestone is included in the Akiyoshi Terrane generated by accretion of seamounts in the trench area. These wheels were identified as *Protocaudina botoni* (Gutschick, 1959) (Ophiocistioidea, Rotasacciidae) and *Thalattocanthus consonus* Carini, 1962 (Holothuroidea, Synaptida, Theeliidae). The diagnosis of the genus *Protocaudina* Croneis, 1932 has been revised to cover all current valid species. The Limestone was deposited as a reef carbonate on a pelagic, shallow-water seamount suggesting that these species habitats were distributed in the pelagic environments.

Key words: microfossils, wheels, Carboniferous, Omi Limestone, *Protocaudina*, *Thalattocanthus*

Introduction

Wheel microfossils are recognizable by their geometric and characteristic shape, with radial spokes and a marginal ring. These are the ossicles found mostly in four extant and fossil families Chiridotidae, Myriotrochidae, Theeliidae and Laetmogonidae of Holothuroidea and in the fossil family Rotasacciidae of Ophiocistioidea (Gilliland, 1993; Boczarowski, 1997). Wheel fossils have been well-known as holothurian ossicles for a long time, but Boczarowski (1997) showed that some of these wheels belong to Ophiocistioidea. From Japan, about eleven species of wheel fossils have been reported from the Lower Silurian to Triassic (Kanasugi, 1979; Iwata *et al.*, 1983), but these studies lacked detailed description of morphology. In this study, we describe two species of wheel fossils, *Protocaudina botoni* (Gutschick, 1959) of Ophiocistioidea and *Thalattocanthus consonus* Carini, 1962 of Holothuroidea, both collected from the Omi Limestone distributed in Itoigawa City, Niigata Prefecture, central Japan.

The wheel fossil of *Protocaudina botoni* from the Carboniferous to Permian in the low to middle latitude of the northern hemisphere, had been known as holothurian ossicles for a long time (Gilliland, 1993). However, the genus *Protocaudina* was transferred from Holothuroidea to the family Rotasacciidae of Ophiocistioidea because the wheels of *Protocaudina* have a button on the concave side and a sieve plate (Boczarowski, 1997, 2001). On the other hand, some researchers suggested that *Protocaudina* is related to the extant deep-sea holothurian family Laetmogonidae in possessing a primary cross on the convex side of wheel ossicles (Gilliland, 1993; Reich, 2012), and the systematic status of *Protocaudina* is still debatable. In this paper, we clearly describe the Japanese specimens of *Protocaudina botoni* for the first time. Moreover, we provide a diagnosis of the genus based on five currently valid species. Boczarowski (1997) fully revised the genus but he had not provided a diagnosis.

Thalattocanthus consonus is known from the Carboniferous to Triassic in a middle latitude of the northern hemisphere (Frizzell & Exline, 1966; Gilliland, 1993). The genus *Thalattocanthus* is monotypic, and distinguished from the other holothurian genera by a single circular depression at the central portion on the convex side of the wheel (Carini, 1962). From Japan this species was also reported from the Ichino-tani and the Oni-maru Formation in the Lower Carboniferous and the Ado-yama Formation in the Upper Triassic with few diagnostic features and a simple sketch (Kanasugi, 1979). We provide a detailed description of a Japanese specimen, along digital microscope images.

Materials and Methods

The fossil wheels were collected at Fukugakuchi, ($36^{\circ}59'14.9''\text{N}$, $137^{\circ}48'00.6''\text{E}$) from the Omi Limestone located in Itoigawa City, Niigata Prefecture, in central Japan; this occupies the eastern end of the Akiyoshi Terrane (Fig. 1). The Omi Limestone extends to 8 km long and 2 km wide, along the Omi and Tomi rivers (Nagamori *et al.*, 2010). The Omi Limestone is characterized by massive and white to gray, carbonate. The fossil locality is composed of boundstone with rich encrusted corals bound with each other, and grainstone (Fig. 2) according to the classification of Dunham (1962), and it is in the range of the *Eostaffella-Millerella* Zone, foraminiferal biozone, in the Upper Carboniferous (Hasegawa & Goto, 1990). Studied ossicles were obtained from the boundstone, which is in the Bashkirian Stage suggested by the conodonts, *Declinognathodus noduliferus* and *D. praenoduliferus*, co-occurring with the present wheel fossils obtained in this study (Personal observation by Y.T.).

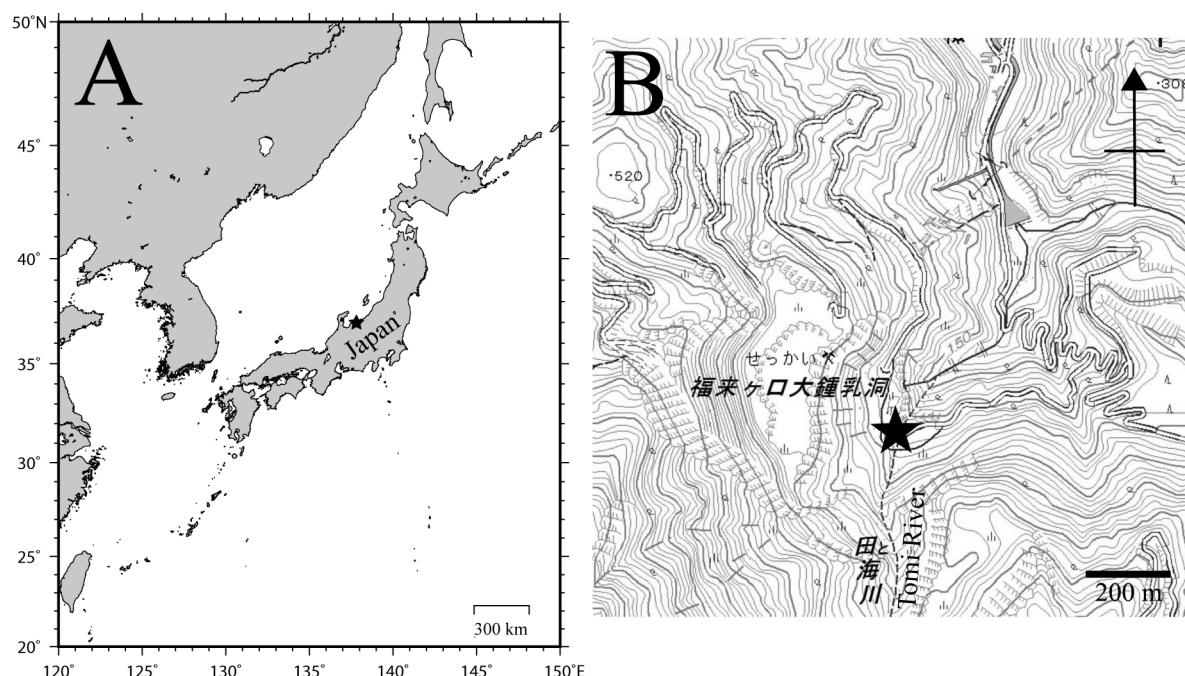


FIGURE 1. Sampling localities. A. Location of Omi Limestone (shown by a star) in Japan. B. Fossil locality (a star) located at the riverbed of the Tomi River. Based on the topographic map “Kotaki” scale 1: 25000 published by the Geospatial Information Authority of Japan.

About 3 kg of limestone blocks were crushed into small pieces, and dissolved with 5–10% acetic acid. The limestone residues were sieved and dried at 40°C in a drying oven, and examined under stereoscopic (Nikon SMZ645) and digital (Keyence VHX-D510) microscope to facilitate picking up wheel fossils with a thin brush. All specimens are deposited in the National Museum of Nature and Science (NMNS), Tsukuba, Japan.

The terminology for wheel ossicles of *Protocaudina* and that of *Thalattocanthus* followed Reich (2012) and Carini (1962), respectively (Fig. 3–4).

TABLE I. Tabular key to the species of the genus *Protocaudina*

Species	Type locality	Type stratum	Outline	Diameter (μm)	Morphology of wheels			Other ossicles	References
					Number of spokes	Spoke shape	Button shape		
<i>P. traguairii</i> Etheridge, 1881	Scotland, U.K.	Lower Carboniferous	oval	254, 280–380	8	narrow, tapering	lower than rim	4	4 equal-sized
<i>P. botoni</i> (Gutschick, 1959)	Indiana, U.S.	Tournaisian, Lower Carboniferous	round or indistinctly undulated	151–390	8	wide, cylindrical	higher than rim	4	4 equal-sized
<i>P. tarazi</i> (Mostler & Rahimi-Yazd, 1976)	Iran	Late Permian	strongly undulated	242	8	short	higher than rim	unknown	unknown
<i>P. sasloensis</i> (Kozur & Mostler, 1989)	Italy	Wordian, Permian	round or indistinctly undulated	259, 265	8	short, tapering	higher than rim	4	2 different sized pairs in point symmetry
<i>P. dulcis</i> Bozarowski, 2001	Poland	Givetian, Middle Devonian	round or oval	160–220	8	narrow, cylindrical	conical shape, with concentric rings	4	2 different sized pairs in point symmetry
									Goniodonts, Pyramids, Sieve plates
									Bozarowski, 2001

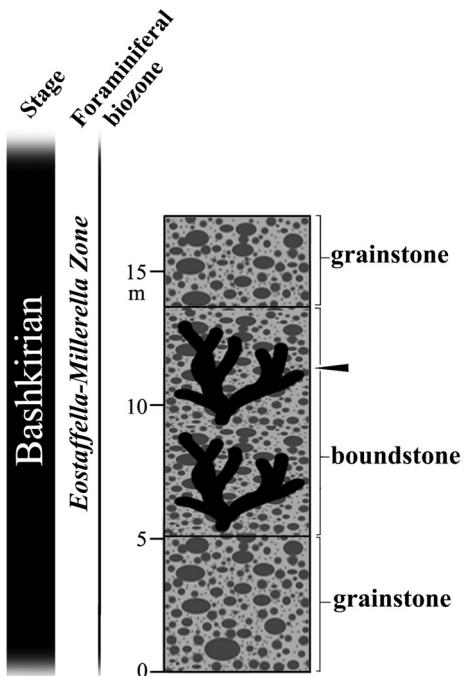


FIGURE 2. Columnar section of the sampling horizon in the Omi Limestone. The limestone is correlated with the *Eostaffella-Millerella* Zone, Bashkirian, and is composed of grainstone and boundstone. The arrow head indicates the horizon of studied wheel ossicles and co-occurring conodonts.

Systematic paleontology

Class Ophiocistioidea Sollas, 1899

Family Rotasacciidae Haude & Langenstrassen, 1976

Genus *Protocaudina* Croneis in Croneis & Mc Cormack, 1932

Type species. *Cheirodota* (?) *traquairii* Etheridge, 1881.

Species included. *P. traquairii* (Etheridge, 1881); *P. botoni* (Gutschick, 1959); *P. tarazi* (Mostler & Rahimi-Yazd, 1976); *P. sosioensis* (Kozur & Mostler, 1989); *P. dulcis* Boczarowski, 2001.

Diagnosis. Calcareous, concavo-convex wheel-like ossicle. Central portion with primary cross on the convex side and button on the concave side. Eight spokes, tapering or of fixed width. Rim outline round or oval, sometimes undulating.

Remarks. The genus *Protocaudina* was established by Croneis (Croneis & Mc Cormack, 1932) for the type species of *Cheirodota* (?) *traquairii* Etheridge, 1881 and *Laetmophasma* (?) *kansasensis* Hanna, 1930. Subsequently, thirteen species have been added to *Protocaudina* (Gilliland, 1993). Etheridge (1881) originally described only the convex side of the wheel and Croneis & Mc Cormack (1932) mentioned nothing about the button on the concave side. Later, Gilliland (1993) confirmed that Etheridge's type specimens of *P. traquairii* have the characteristic button on the concave side, and Boczarowski (1997) revised *Protocaudina*, including only *P. traquairii* and three species with eight spokes transferred from *Microantyx* Kornicker & Imbrie, 1958, and he excluded the other fourteen species, which lacked the buttons, from this genus. However, he did not provide an emended diagnosis of the genus. Subsequently, another species *Protocaudina dulcis* was described in this genus (Boczarowski, 2001). Thus five species currently belong to *Protocaudina* (Table 1).

***Protocaudina botoni* (Gutschick, 1959)**

Figure 3

Microantyx botoni Gutschick, 1959: 134–135, Pl. 26 (Figs. 22–23, 28–29), Text-fig. 3

Microantyx botoni—Frizzell & Exline, 1966: U668; Gutschick *et al.*, 1967: 1472–1473, Pls. 186 (Figs. 41–51), 187 (Fig. 16); Nabavi & Hamdi, 1975: 14–15, Pl. 3 (Figs. 1–4); Mostler & Rahimi-Yazd, 1976: 22, Pl. 1 (Figs. 1–5, 7, 11)

Protocaudina botoni—Boczarowski, 1997: 334

Non *Microantyx botoni*—Alexandrowicz, 1971: 287–289, Text-figs. 2(3–4); Mostler, 1971: 10, Pl. 2 (Figs. 16–17); Ding, 1985: 344, Pl. 1 (Figs. 12–13, 16), Text-fig. 4

Material examined. Four specimens (NMNS PA-18633–18636) collected from the *Eostaffella-Millerella* Zone, Lower Pennsylvanian; Omi Limestone, Niigata, Japan.

Description. Wheels, concavo-convex, circular, perimeter sometimes slightly undulating, 151–269 µm in diameter. Central pores four, of equal size and oval in shape. Connecting central portion 96–134 µm in diameter, occupying 43–64% of wheel diameter. Spokes eight in number, short and fixed width. Marginal ring is rolled slightly inward. Button on the concave side of central portion prominent, higher than rim. Rim width 11–26 µm, occupying 6.9–9.6% of wheel diameter. No other elements identified.

Occurrence. The Rockford Limestone Formation, Lower Mississippian: Indiana, U.S.A. (Gutschick, 1959.). The Madison Group, Mississippian: Montana, U.S.A. (Gutschick *et al.*, 1967); the Ruteh Formation, Middle to Upper Permian: Semnan, Iran (Nabavi & Hamid, 1975); Dzhulfian (the *Codonofusiella-Paratirolites* Zone), boundary section of Permian and Triassic: Julfa, Azerbaijan (Mostler & Rahimi-Yazd, 1976); the *Eostaffella-Millerella* Zone, Lower Pennsylvanian: Niigata, Japan (present study).

Remarks. Morphological comparison of *Protocaudina botoni* with the valid congeneric species is provided in Table 1. There have been some misidentified and doubtful records of this species. Alexandrowicz (1971) reported *P. botoni* from Southern Poland, but the specimens reported in his study were actually identified as *Protocaudina sosioensis* because they have two different-sized central pores (Kozur & Mostler, 1989). Mostler (1971) and Ding (1985) also reported this species, but the reported specimens are probably assigned either to *Protocaudina traquairii* (Etheridge, 1881) or to *P. sosioensis*, because of their short spokes. The descriptions of *Microantyx* cf. *botoni* from Azerbaijan (Mostler & Rahimi-Yazd, 1976), of the Chinese specimens by Zhan (1986) and of the Japanese specimens by Kanasugi (1979) are not detailed enough to enable identification of their specimens. We did not include these doubtful records in the synonym list.

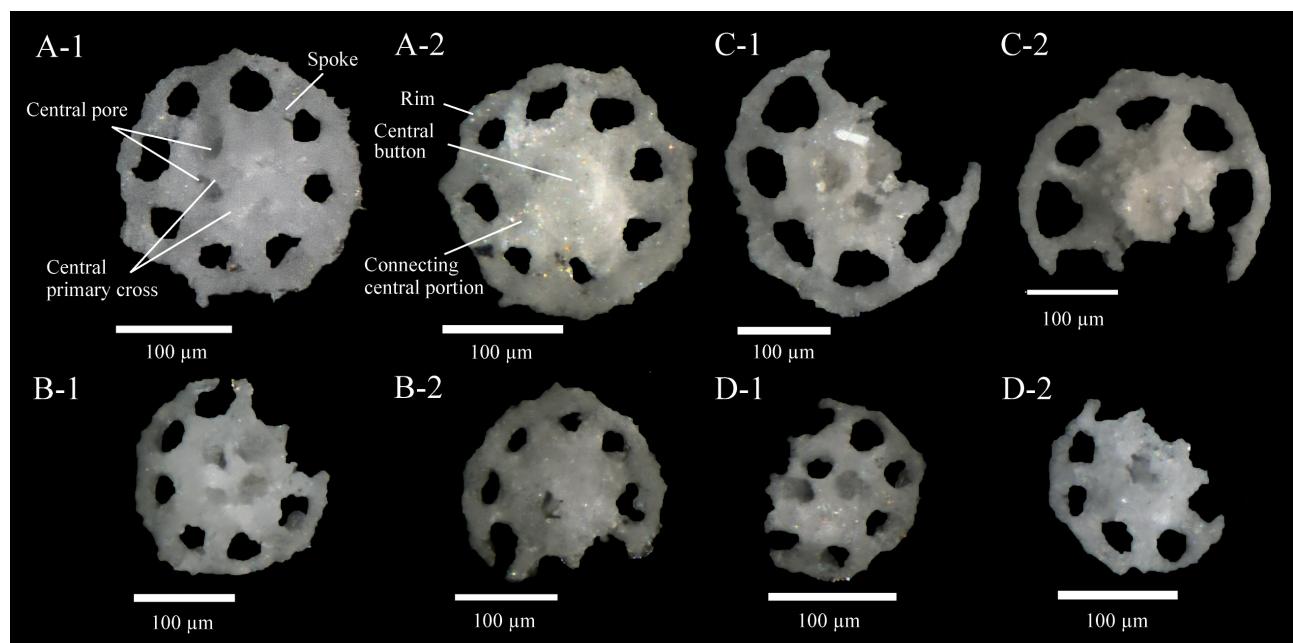


FIGURE 3. Wheel ossicles of *Protocaudina botoni*. A. NMNS PA-18633. B. NMNS PA-18634. C. NMNS PA-18635. D. NMNS PA-18636. Left (1) and right (2) photographs show convex and concave sides, respectively.

The size of the present specimens ranges from 151–269 µm (151, 190, 202 and 269 µm) in diameter, and the last wheel was much larger than the others. Nabavi and Hamdi (1975) reported Iranian specimens with bimodal size distribution of the wheel diameters. Some recent laetmogonid species have also bimodal size distribution in the wheel diameters (*e. g.* *Laetmogone maculata* (Théel, 1879), *Pannychia moseleyi* Théel, 1882; Hansen, 1975). There is a possibility that *P. botoni* also had bimodal distribution in the wheel diameters unlike that of the other congeneric species.

Class Holothuroidea de Blainville, 1834

Order Synaptida Cuénot, 1891

Family Theeliidae Frizzell & Exline, 1955

Genus *Thalattocanthus* Carini, 1962

***Thalattocanthus consonus* Carini, 1962**

Figure 4

Thalattocanthus consonus Carini, 1962: 392–394, Pl. 1 (Figs. 1–23), Text-figs. 1–7

Thalattocanthus consonus—Frizzell & Exline, 1966: U668, Text-fig. 533.8; Gutschick *et al.*, 1967: 1471–1472, Pls. 186 (Figs. 1–8), 187 (Figs. 28, 35), Text-fig. 3; Mostler, 1971: 10, Pl. 2 (Figs. 9–14); Kanasugi, 1979: 162–164, Pl. 2 (Fig. 5), Tab. 1; Ding, 1985: 344, Pl. 1 (Figs. 7, 10–11), Text-fig. 3

Description. Wheel concavo-convex, rounded polygonal in outline, 170 µm in diameter. Central portion 74 µm in diameter, occupying 43% of wheel diameter, with single circular central depression on convex side. Brim of central depression elevated circular. Spokes six, square, but slightly tapering towards rim. Wheel without denticulation on the inner brim of the rim. Rim width 16 µm, occupying 9.6% of wheel diameter, narrower than spoke width. Button on the concave side of central portion prominent and higher than rim.

Material examined. One specimen (NMNS PA-18637) collected from the *Eostaffella-Millerella* Zone, Lower Pennsylvanian; Omi Limestone, Niigata, Japan.

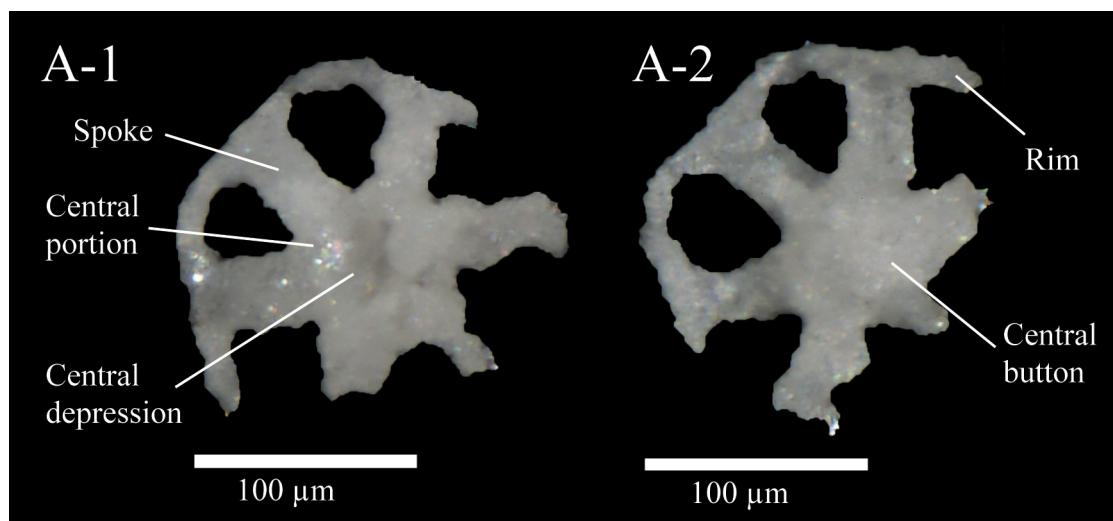


FIGURE 4. Wheel ossicle of *Thalattocanthus consonus*. A. NMNS PA-18637. Left (1) and right (2) photographs show convex and concave sides, respectively.

Occurrence. The *Fenestella* brachiopods Zone, Mississippian: Dasht-i-Nawar Valley, Afghanistan (Mostler, 1971); the Madison Group, Mississippian: Montana, U.S.A. (Gutschick *et al.*, 1967); the Chouteau Group, Mississippian: Missouri, U.S.A. (Gutschick *et al.*, 1967); Upper Desmoinesian (Upper

Carboniferous): Oklahoma, U.S.A. (Carini, 1962); the Taiyuan Formation, Upper Carboniferous: Henan, China (Ding, 1985); Lower Carboniferous: Ichino-tani, Gifu and Oni-maru, Iwate, Japan (Kanasugi, 1979); Upper Triassic: Ado-yama, Tochigi, Japan (Kanasugi, 1979); Anisian: locality unknown (Mostler, 1971); Dolomites, Northern Alps: age unknown (Mostler, 1971); the *Eostaffella-Millerella* Zone, Lower Pennsylvanian: Niigata, Japan (present study).

Remarks. The wheel of *Thalattocanthus consonus* is distinguished from other synaptid wheels by a single circular depression on the central portion and denticulation on the inner brim of rim (Gilliland, 1993). The single circular depression was evident in our specimen, but the denticulation on the inner brim of rim was not observed because of poor preservation of rim. Mostler (1971) reported wheels without denticulation from Afghanistan. Further studies are required to clarify whether or not these wheels without denticulation are conspecific with this species.

Paleogeography

The Akiyoshi Terrane that includes the Omi Limestone where the present specimens were collected is located along a subduction trench (Isozaki *et al.*, 2010), and is composed of pelagic reef carbonate (Ota, 1968). The terrane is a subduction-generated accretionary complex, which consists of tectonic aggregate of oceanic and terrigenous rocks (Kanmera & Nishi, 1983). The Omi Limestone is pure reef carbonate without terrigenous clastic materials, underlined by basaltic volcanoclastic rocks. Nakazawa (2001) interpreted that the Omi Limestone was deposited on the top of a pelagic seamount. Brachiopod fauna and paleomagnetic data suggest that the seamount was located at low to mid latitude of the northern Panthalassa Ocean in the Carboniferous (Fujiwara, 1967; Tazawa *et al.*, 2005).

These fossil species, *Protocaudina botoni* and *Thalattocanthus consonus*, were previously recorded only from continental margin areas (see Occurrences). In the present study, these species were recorded from a shallow-water deposit on a pelagic seamount, suggesting that these species were widely distributed not only in continental margin but also in pelagic oceanic setting. These species might have long-distance dispersal potential.

Acknowledgements

We thank Mr. Y. Kamikawa (Taiheiyo Cement Corporation) and Mr. Y. Egawa (Myojyo Cement Co., Ltd.) who allow and help Y.T. to survey and collect the material in their mine, Prof. K. Sashida and Dr. S. Agematsu (University of Tsukuba) who provided the opportunity to do this study, and Dr. Y. Ishida (Suginami-ku, Tokyo), Dr. S.P. Woo (Universiti Sains Malaysia) and Dr. A. Martynov (Zoological Museum, Moscow State University) for their comments on the manuscript and kind help in literature search. We also appreciate Dr. D.L. Pawson (National Museum of Natural History, Smithsonian Institution) and Prof. T. Oji (Nagoya University Museum, Nagoya University) for their generous reviewing and valuable comments to improve the manuscript. A.O. is supported by the Research Institute of Marine Invertebrates (IKU-4, 2017).

References

- Alexandrowicz, Z. (1971) Carboniferous Holothuroidea sclerites in the Upper Silesia Coal Basin (Southern Poland). *Rocznik Polskiego Towarzystwa Geologicznego [= Annales de la Societe Geologique de Pologne]*, 41 (2), 281–291.
- Blainville, H.M.D. (1834) *Manuel d'actinologie ou de zoophythologie*. Levraut, F.G. Paris, 694 pp.
<https://doi.org/10.5962/bhl.title.8768>
- Boczarowski, A. (1997) Mistaken identity of wheel-shaped sclerites of Ophiocistioidea and Holothuroidea. *Slovak Geological Magazine*, 3 (4), 331–340.
- Boczarowski, A. (2001) Isolated sclerites of Devonian non-pelmatozoan echinoderms. *Palaeontologia Polonica*, 59, 3–220.
- Carini, G.F. (1962) A new genus of holothurian sclerite from the Wewoka shale of Oklahoma. *Micropaleontology*, 8 (3), 391–395.
<https://doi.org/10.2307/1484529>
- Croneis, C. & Mc Cormack, J. (1932) Fossil Holothuroidea. *Journal of Paleontology*, 6 (2), 111–148.

- Cuénot, L. (1891) Études morphologiques sur les Echinodermes. *Archives de Biologie*, 11, 313–680.
- Ding, H. (1985) Discovery of holothurian sclerites from the Taiyuan Formation (Upper Carboniferous), Henan, China. *Weitigushengwu-xuebao* [= *Acta Micropalaeontologica Sinica*], 2 (4), 339–350.
- Dunham, R.J. (1962) Classification of carbonate rocks according to depositional textures. *Memoir. American Association of Petroleum Geologists*, 1, 108–121.
- Etheridge, R. (1881) On the presence of the scattered skeletal remains of Holothuroidea in the Carboniferous limestone series of Scotland. *Proceedings of the Royal Physical Society of Edinburgh*, 6, 183–198.
- Frizzell, D.L. & Exline, H. (1955) Monograph of fossil holothurian sclerites. *Bulletin. University of Missouri, School of Mines and Metallurgy (Technical Series)*, 89 (1), 1–204.
- Frizzell, D.L. & Exline, H. (1966) Holothuroidea—Fossil record. In: Moore, R.C. (Ed), *Treatise on Invertebrate Paleontology*, U, *Echinodermata 3 [Asterozoa-Echinozoa] (2)*. The Geological Society of America, Inc. and University of Kansas Press, New York, pp. U646–U672.
- Fujiwara, Y. (1967) Palaeomagnetism of Upper Carboniferous Rocks in Akiyoshi Province, S.W. Honshu, Japan. *Journal of the Faculty of Science, Hokkaido University. Series 4, Geology and mineralogy*, 13 (4), 395–399.
- Gilliland, P.M. (1993) The skeletal morphology, systematics and evolutionary history of holothurians. *Special papers in Paleontology*, 47, 1–147.
- Gutschick, R.C. (1959) Lower Mississippian holothurian sclerites from the Rockford Limestone of northern Indiana. *Journal of Paleontology*, 33 (1), 130–137.
- Gutschick, R.C., Canis, W.F. & Brill, K.G. Jr. (1967) Kinderhook (Mississippian) holothurian sclerites from Montana and Missouri. *Journal of Paleontology*, 41 (6), 1461–1480.
- Hanna, G.D. (1930) Remains of Holothuroidea from the Carboniferous of Kansas. *Journal of Paleontology*, 4 (4), 413–414.
- Hansen, B. (1975) Systematics and biology of the deep-sea holothurians. Part I. Elasipoda. *Galathea Report*, 13, 1–262.
- Hasegawa, Y. & Goto, M. (1990) Paleozoic and Mesozoic in the Omi area, Niigata Pref. 97th Annual Meeting of the Geological Society of Japan excursion guidebook, 227–260.
- Haude, R. & Langenstrassen, F. (1976) *Rotasaccus dentifer* n. g. n. sp., ein devonischer Ophiocistioide (Echinodermata) mit „holothuroiden“ Wandskleriten und „echinoidem“ Kauapparat. *Paläontologische Zeitschrift*, 50, 130–150.
<https://doi.org/10.1007/BF02987690>
- Isozaki, Y., Aoki, K., Nakama, T. & Yanai, S. (2010) New insight into a subduction-related orogen: a reappraisal of the geotectonic framework and evolution of the Japanese islands. *Gondwana Research*, 18 (1), 82–105.
<https://doi.org/10.1016/j.gr.2010.02.015>
- Iwata, K., Uozumi, S., Nakamura, K. & Tajika, J. (1983) Discovery of radiolarians and holothurian sclerites from the Pre-Tertiary System around Nishiokoppe, northeast Hokkaido (Preliminary report). *The Journal of the Geological Society of Japan*, 89 (1), 55–56.
<https://doi.org/10.5575/geosoc.89.55>
- Kanasugi, H. (1979) Nihonsan-namako-no-koppen-kaseki [= Fossils of holothurian ossicle from Japan]. In: Kanuma-Mosaburo-kyoujuu-taikan-kinenkai (Ed.), *Biostratigraphy of Permian and Triassic. conodonts and holothurian sclerites in Japan*. Tokyo, pp. 159–169.
- Kanmera, K. & Nishi, K. (1983) Accreted oceanic reef complex in southwest Japan. In: Hashimoto, M. & Ueda, S. (Eds.), *Accretion Tectonics in the Circum-Pacific Regions*. Terra Scientific Publishing Company, Tokyo, pp. 195–206.
https://doi.org/10.1007/978-94-009-7102-8_14
- Kornicker, L.S. & Imbrie, J. (1958) Holothurian sclerites from the Florena shale (Permian) of Kansas. *Micropaleontology*, 4 (1), 93–96.
<https://doi.org/10.2307/1484255>
- Kozur, H. & Mostler, H. (1989) Echinoderm Remains from the Middle Permian (Wordian) from Sosio Valley (Western Sicily). *Jahrbuch der Geologischen Bundesanstalt*, 132 (4), 677–685.
- Mostler, H. (1971) Mikrofaunen aus dem Unter-Karbon vom Hindukusch. *Geologisch-Paläontologische Mitteilungen Innsbruck*, 1 (12), 1–19.
- Mostler, H. & Rahimi-Yazd, A. (1976) Neue Holothuriensklerite aus dem Oberperm von Julfa in Nordiran. *Geologisch-Paläontologische Mitteilungen Innsbruck*, 5 (7), 1–35.
- Nabavi, M.H. & Hamdi, B. (1975) Permian limestone with holothurian sclerites, Semnan area, south-central Alborz, Iran. *Report. Geological Survey of Iran*, 32, 5–17.
- Nagamori, H., Takeuchi, M., Furukawa, R., Nakazawa, T. & Nakano, S. (2010) *Geology of the Kotaki district. Quadrangle Series, 1:50,000*. Geological Survey of Japan, AIST, Tsukuba, 130 pp.
- Nakazawa, T. (2001) Carboniferous reef succession of the Panthalassan open-ocean setting: example from Omi Limestone, central Japan. *Facies. Institut für Paläontologie der Universität Erlangen-Nürnberg*, 44, 183–210.
<https://doi.org/10.1007/BF02668174>

- Ota, M. (1968) The Akiyoshi Limestone Group: A geosynclinal organic reef complex. *Bulletin of the Akiyoshi-dai Science Museum*, 5, 1–44.
- Reich, M. (2012) On Mesozoic laetmogonid sea cucumbers (Echinodermata: Holothuroidea: Elasipodida). *Zoosymposia*, 7, 185–212.
- Sollas, W.J. (1899) Fossils in the University Museum, Oxford: I. On Silurian Echinoidea and Ophiuroidea. *Quarterly Journal of the Geological Society of London*, 55, 692–715.
<https://doi.org/10.1144/GSL.JGS.1899.055.01-04.41>
- Tazawa, J., Sato, K. & Takenouchi, K. (2005) *Delepinea* and *Daviesiella* (Chonetida, Brachiopoda) from the Lower Carboniferous of Omi, central Japan. *Science Reports of Niigata University. Series E, (Geology)*, 20, 1–13.
- Théel, H. (1879) Preliminary report on the Holothuroidea of the exploring voyage of H.M.S. “Challenger”, under Professor Sir C. Wyville Thomson. Part I. *Bihang till K. Svenska Vetenskaps-Akademiens handlingar*, 5 (19), 1–20.
- Théel, H. (1882) Report on the Holothuroidea dredged by the H.M.S. Challenger, during 1873–76. Part I. *Report of the Scientific Results of the Voyage of H.M.S. Challeger during the year 1873–76 Zoology*, 4 (3), 1–176.
- Zhang, J. (1986) Lower Carboniferous holothurian sclerites from Hunan Province. *Weiti-gushengwu-xuebao [= Acta Micropalaeontologica Sinica]*, 3 (4), 399–408.